BEHAVIORAL SYNDROMES AND THEIR EFFECT ON DISPERSAL IN *NOTONECTA IRRORATA*

By

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Dispersal is an important life-history characteristic for many organisms, including in the genus of back-swimming insect *Notonecta*. The propensity to disperse is a behavior that might be affected by an individual's other behavioral tendencies. Correlated behavioral traits, or behavioral syndromes, are evidence for personality in animals and could potentially play a role in dispersal propensity. This research examined whether or not a behavioral syndrome exists in *Notonecta irrorata* and whether or not these levels of behavior 1) influenced dispersal, 2) were consistent through time, and 3) were consistent when other conspecifics were present. I found that a behavioral syndrome does exist in the foraging behaviors of *N. irrorata* (swimming time, vegetation use, number of prey consumed, and perching depth). These four traits were correlated along a "boldness gradient" and individuals were sorted into personality types based on where they fell along this bold/passive axis. Bold individuals spent, on average, more time swimming, used vegetation less, consumed more prey items, and perched at shallower depth in the water than passive individuals did. Dispersal propensity was influenced by the type of personality (bold or

passive) of an individual. Specifically, passive individuals dispersed from experimental pools more quickly on average than bold individuals, and the dispersal propensity of each personality type was influenced by the personality type of other conspecifics present in the pool. The average levels of each foraging behavior remained consistent through time and were not affected by the presence of another individual, even though the presence of other individuals did affect dispersal behavior in each personality type. This research shows that behavioral consistency is evident in *Notonecta* and highlights the importance of recognizing animal personality as a legitimate factor in population and meta-population dynamics.

BEHAVIORAL SYNDROMES AND THEIR EFFECT ON DISPERSAL IN *NOTONECTA IRRORATA*

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CHAPTER I

INTRODUCTION

Dispersal in animals is an important life-history trait that affects spatially-structured population dynamics, gene flow, species distributions, and the ability of species to track environmental change (Bowler & Benton 2005; Cote et al. 2010a). There are many reasons an individual may choose to disperse. Individuals may leave a habitat to look for more available food resources or shelter, to avoid competition due to high population densities or a skewed sex ratio, or to avoid a high-predation habitat patch. It can also be evolutionarily advantageous for an individual to disperse away from a natal habitat due to the risk of inbreeding or competition among close relatives (Hamilton and May 1997). In some cases, particularly for organisms with complex life histories (e.g. amphibians, dipterans, etc.), dispersal is required in order to complete an individual's life cycle. The decision to disperse can be risky due to several factors an organism must consider. Foremost, dispersal is energetically costly (Bonte et al. 2012). An individual that is starving due to high competition for food resources may be inclined to find food elsewhere, however, it may not have the energy to disperse very far. On the other hand, dispersing to a relatively unpopulated habitat patch may mean the difference between finding food and starvation. Dispersal may also make it more difficult for individuals to avoid predators in the habitat matrix they disperse through (Yoder et al. 2004) since activity level is related to predation risk (Lima 1998). Even if an individual is choosing to leave a high-predation environment, dispersing away from their habitat may mean giving up any shelter they had and exposing the individual to more predators. Individuals may have to weigh the relative mortality risk within a patch to the risk of

traveling between patches. There is also no guarantee of greater resources or a better-quality habitat within the dispersal range of an individual.

Although dispersal is an integral part of many animal populations, the determination of if and when to disperse is often a behavioral decision made by individuals. Individuals must make the decision to leave a habitat in search of another, but not all individuals of a population will make this decision in the exact same way. It has long been suggested that dispersers are not just a random subset of a population and that they must have some qualitative differences distinguishing them from non-dispersers, including potential behavioral differences (Myers and Krebs 1971; Cote et al. 2017b). The tendency for an individual to leave a patch, known as dispersal propensity, may be contingent on an animal's other behavioral tendencies i.e. personality or behavioral syndromes (Sih et al. 2012). Behavioral syndromes are a suite of correlated behaviors within a species that an individual is predisposed to (Sih et al. 2003). Behavioral syndromes can be represented as an axis of change, and opposite ends of the axis could correspond to individuals that are less likely (i.e., passive) or more likely (i.e., bold) to engage in a broad suite of correlated behaviors. Some hypothesize that individuals with certain behavioral traits - high activity levels, boldness, and low sociability - are more prone to disperse and colonize new habitats (Fraser et al. 2001; Cote et al. 2010a; Cote et al. 2010b). Other studies have found that shy, passive individuals are more likely to disperse (Found and St. Clair 2016). It is unclear yet which personality types are better suited for dispersal, or if it depends on the species. However, these findings suggest that dispersal rates within a given species may be predictable if other behaviors of individuals within the population are known.

If an individual's personality affects its dispersal propensity, then we might expect the overall behavioral makeup of other individuals in the population to also play a role. Group social

dynamics can have large-ranging effects on any one individual (Sih and Watters 2005). One example of this is in the water strider, *Aquarius regimis*, where groups of individuals that were mostly made up of very active and aggressive individuals had lower mating success than groups made up of less active and non-aggressive individuals (Sih and Watters 2005). This example shows that an individual's chance of mating success in the patch is dependent on the personality of other conspecifics within the patch. This suggests that individuals might perceive the quality of a habitat patch differently depending on the personality types already present. The presence of many bold, active individuals might imply that there is a lack of predators in the patch since activity levels of individuals tend to increase with decreased predation risk (Lawler 1989; Skelly 1994). Having more active personality types in the pond could make it appear that the individuals have raised their activity level. This could make individuals want to stay in the patch because of the perceived low predation risk. Likewise, the presence of mainly passive, inactive individuals might make the patch seem emptier or resource-poor. A seemingly conspecific-empty patch, where most of the individuals hide in vegetation more and swim less often, could imply that other organisms (i.e. predators or competitors) are more abundant and so individuals might want to disperse elsewhere.

In this study, I evaluated whether the dispersal propensity of an individual was related to its personality. I used *Notonecta irrorata* to test three hypotheses: 1) *N. irrorata* has a behavioral syndrome that causes different foraging behaviors to be correlated with each other, 2) different behavioral types (BTs) exhibit different dispersal propensities, and 3) dispersal propensity will depend on the BT of other individuals present in the population. *Notonecta* are useful organisms to ask these questions because they are semi-aquatic and flight-capable, meaning that they can spend the entirety of their life in one freshwater pond if they choose but can also make the decision to disperse (fly) from a water body in search of another. They are also frequently found in high

densities within a pond (Streams 1987; personal observations), suggesting that they intermingle with conspecifics quite regularly.

MATERIALS AND METHODS

I performed a set of experiments to evaluate the presence of a behavioral syndrome in *N. irrorata* and to test hypotheses that 1) the propensity of an individual to disperse away from a habitat stems from this behavioral syndrome, and 2) the co-occurrence of individuals with different behavioral types will alter the dispersal propensity of an individual.

Assays of foraging behavior

I observed the foraging behavior of 450 *N. irrorata* individuals. I performed assays over the course of five two-day periods (each two-day period is referred to as a block). For each two-day period I performed assays on 90 individuals, with 45 individuals being observed on each of the days. Collection of *N. irrorata* from natural ponds took place periodically between May 27th and July 22nd, 2017. For each block, 90 individual *N. irrorata* were collected using dip-nets over the course of one day from ponds in the Croatan National Forest (35°02'53.1"N, 77°03'05.8"W) and transferred into closed buckets of pond water at a density of 25-35 individuals per bucket for transport back to East Carolina University. Upon return to the lab, each *N. irrorata* was transferred into a labeled plastic container filled with approximately 470 mL of pond water and one or two sticks as perches.

Behavioral observations were conducted on two successive days following collection. *Notonecta* were starved between the time of collection and the start of behavioral observations.

Each individual's behavior was observed in one of five 15-gallon aquaria (60 cm x 30 cm x 33 cm) filled 25 cm high with reverse osmosis treated (RO-rite) tap water. A simulated vegetative refuge was placed on one side of each tank by hanging 14 pieces of frayed coconut husk rope that extended from the top of the tank to the bottom. Frayed rope was hung from the water surface on one side of the aquarium to the aquarium bottom to serve as artificial vegetation. The vegetative refuge made up about 20% of the space in the aquarium with the rest of the space consisting of open water. All tanks were placed onto shelves and surrounded with black boards on three sides to prevent individuals from seeing one another. One side of each tank was left open so that I could observe each individual. Every tank had centimeter depth lines written in marker on each open side to facilitate the measurement of perching depth of individuals.

Observations were made once in the morning beginning at approximately 8 A.M. and once in the afternoon beginning at approximately 2 P.M., for a total observation time of ten minutes for each individual. After being placed into aquaria, individuals were allowed 35-40 minutes to acclimate before being observed (following Streams 1987). Three behaviors (swimming time, resting time at surface, vegetation use, and perching depth) were observed and recorded using the program JWatcher v1.0 (Blumstein and Daniel 2007). Swimming time was measured as the amount of time an individual spent actively moving around the tank. Vegetation use was measured as the amount of time an individual spent associating itself (perching or swimming in it) with the artificial vegetation. Perching depth was measured as the average depth in centimeters an individual perched either on the vegetation or on the sides of the tank, weighted by the amount of time they spent at each perch. After the five minute period, the individual was dip-netted out of the water and put back into the plastic pint container, and a new individual was placed into the tank.

After observing the swimming, resting and perching behavior of *Notonecta*, I transferred each individual into their own 20 cm x 32.5 cm x 11.5 cm plastic container containing 470 mL of water and five 3rd to 4th instar larval *Aedes aegypti*. To estimate the foraging efficiency of an individual *Notonecta*, I counted the number of *A. aegypti* larvae eaten within four hours.

Once all behavioral data were collected for individuals within a block, I performed a Principal Components Analysis (PCA) using SAS Enterprise Guide (SAS Institute, Cary NC) on the correlation matrix for the four traits mentioned above. I used a PCA in order to reduce the four correlated traits into a smaller set of axes that could be interpreted. The first principal component axis (PC1), which always explains the greatest amount of variance in the data, represents a gradient of correlated behaviors and differences in PC scores among individuals reflect how they differ in these correlated behaviors. I refer to this axis as a "boldness" gradient because the correlations of behaviors with the scores of this gradient indicate that lower scores correspond to individuals that had more bold characteristics (higher swimming time, lower vegetation use, shallower perch depth, and less prey remaining; see results and Figure 1.1 for details).

Individuals were then sorted on the basis of their PC1 scores and those with the highest 30 PC1 scores were classified as "passive" and those with the smallest 30 PC1 scores were classified "bold" (Figure 1.2). This was done 1) to evaluate whether individuals assigned to different behavioral types differed in their individual behaviors and 2) because these individuals would be used in a follow-up experiment designed to examine whether the dispersal propensity of an individual was related to the individual's BT and the BT of other individuals that are present.

All assigned individuals were tagged with a unique number tag on the day immediately following the second behavioral observation day within a block. To apply these tags, an individual was taken out of the water and held in place on a benchtop using a small piece of flexible square

mesh with a 5 x 5 mm opening in the middle. A toothpick was used to superglue a laser-printed, water-resistant paper tag (4 mm x 2 mm) onto the pronotum of an individual. The individual was left under a petri dish lid for approximately two minutes to allow the superglue to dry before being placed back into the water.

A comparison of the PC1 scores between the two personality types was run using a generalized linear mixed model (GLMM) in order to treat block as a random effect and incorporate a block by personality interaction term. The model was fitted using restricted maximum likelihood estimation (REML) with a variance components covariance structure and the Kenward-Rogers method for computing denominator degrees of freedom. I compared each behavior between the two personality types using the same GLMM for each behavioral response variable.

Dispersal Experiments

I ran an experiment that addressed the hypotheses that 1) the propensity of an individual to disperse away from a habitat is influenced by a behavioral syndrome, and 2) the dispersal propensity of a behavioral type is contingent on whether individuals of a different behavioral type are present. For each block corresponding to the same PCA blocks above, three experimental mesocosms were set up two feet apart in an open field at East Carolina University's West Research Campus (35°37'57.0"N, 77°28'56.1"W). This location was about 20-30 meters away from an ephemeral ditch. Mesocosms were created using plastic wading pools (91 cm wide by 20.5 cm deep). Each pool was prepared by filling to a depth of approximately 16 cm of dechlorinated tap water, adding 300 grams of leaf litter, and inoculating with zooplankton collected from a nearby artificial drainage pond. The zooplankton were added two days after the initial filling of the pools to allow sufficient time for the water to be dechlorinated. Each pool was left uncovered and

undisturbed for at least 12 days prior to *N. irrorata* introduction to allow for natural colonization of other invertebrates and growth of the zooplankton colony.

For each time period (block), 60 individually-marked *N. irrorata* were randomly assigned in groups of twenty to one of three treatment pools (twenty bold individuals, twenty passive individuals, or a mix of ten bold and ten passive individuals) according to their behavioral group. Beginning on the morning immediately following introduction, each pool was exhaustively dip-netted daily to search for remaining *Notonecta*. The tag numbers of all found individuals were recorded. Vegetation was taken out and searched through so as not to miss individuals underwater. All found individuals were put back into the pools that they were taken from along with all of the leaf litter. Dead individuals were removed from the pools and not counted as dispersers, though this only happened to three individuals out of all blocks. Pools were checked daily until there were no remaining *Notonecta* in a pool.

All analyses were performed in SAS Enterprise Guide (SAS Institute, Cary NC). Differences in the proportion of individuals that had dispersed between the three treatment pools were evaluated using a Generalized Linear Model in PROC GENMOD. The model specified a binomial distribution and logit link function and an autoregressive covariance structure. Probability values evaluating differences in the least squares mean estimates among treatment pairs were adjusted using the Tukey-Kramer method to control the experiment-wise error rate.

Differences in the average time to dispersal of individuals within a pool were evaluated using PROC MIXED. I used a GLMM that was fitted using REML with a variance components covariance structure and the Kenward-Rogers method for computing denominator degrees of freedom. I included treatment as a fixed effect and block as a random effect with a block by treatment interaction as the subject.

Differences in the time to disperse on the basis of an individual's PC1 score were evaluated using PROC MIXED. I used a GLMM that was fitted using REML with a variance components covariance structure and the Kenward-Rogers method for computing denominator degrees of freedom. I included PC1 score as a fixed effect and block as a random effect.

RESULTS

Test for Behavioral Syndrome

The first principal component axis explained on average 42% of the variation in foraging behavior and all four behaviors loaded heavily on this axis (Figure 1.1). Swimming time was negatively correlated to PC1 scores, while the other three behaviors (vegetation use, prey remaining, and perch depth) were positively correlated to PC1 scores. In general, higher PC1 scores were associated with lower swimming time, higher vegetation use, higher number of prey remaining, and deeper perching depth.

I observed substantial among-individual variation in PC1 scores but there were not discrete groupings of individuals based on these scores (Figure 1.2). Nonetheless, I classified 1/3 of these individuals as "passive" (those with the highest PC 1 scores) and another 1/3 as "bold" (those with the lowest PC 1 scores) and these two groups differed in their Principal Component 1 scores ($F_{1, 8}$ = 757.01, $p < 0.001$). Individuals that were classified as "bold" on average swam approximately seven times longer ($F_{1, 8}$ = 52.63, $p < 0.001$), used vegetation a third as often ($F_{1, 8}$ = 52.09, $p < 0.001$), perched 5.5 cm shallower in the water column ($F_{1, 8}$ = 5.43, $p = 0.048$), and were 40% more efficient at capturing prey ($F_{1, 8}$ = 22.35, $p = 0.002$) than individuals that were classified as "passive" (Figures 1.3-1.6).

Dispersal Experiments

The proportion of individuals that dispersed away from a mesocosm depended on the interactive effect of time and treatment ($Z = -2.33$, $p = 0.02$). Treatments differed in the proportion of individuals that dispersed away from a mesocosm between 2 and 5 days after individuals were added to mesocosms but not 1 or 6 days after individuals were introduced to mesocosms (Figure 1.7). The proportion of individuals that dispersed from the mixed treatment was intermediate to but did not differ significantly from that observed in either the all-bold or all-passive treatments throughout the duration of the study ($p \geq 0.0918$); however, a higher proportion of individuals tended to disperse away from passive treatments than bold treatments on days 2 ($p = .035$), 3 ($p = .0145$), 4 ($p = .0129$), and 5 ($p = .0131$). After six days, nearly all individuals regardless of personality type had dispersed.

Individuals with a higher PC1 score (reflecting a lower level of boldness) spent less time within a pool before dispersing than individuals with a lower PC1 score ($F_{1, 190} = 31.44$, $p < .001$; Figure 1.8). PC score explained 11% of the among-individual variation in time to dispersal. Individuals that were in the passive treatment dispersed faster (time to dispersal: 2.6 days ± 0.236) than individuals that were in the bold treatment (time to dispersal: 3.4 days ± 0.236) ($F_{1, 8.02} = 5.57$, $p = 0.0458$).

Bold individuals were more than twice as likely to disperse away from a pond by day 2 when they co-occurred with passive individuals than when they did not (proportion dispersed in all-bold: 0.212, proportion dispersed in mixed: 0.4437; $Z = -1.97$, $p = 0.0494$). Dispersal by bold individuals was about 20% greater in general when they were mixed with passive individuals, but these differences were only statistically meaningful on day 2 (Figure 1.9). In contrast, passive

individuals that did not co-occur with bold individuals were more likely to disperse by day 3 than passive individuals that co-occurred with bold individuals (Figure 1.10).

DISCUSSION

Variation in dispersal has been studied extensively in the past (e.g. optimal foraging theory-Charnov 1976), but only recently has the idea of personality-dependent dispersal in animals been discussed in much detail (Bowler and Benton 2005; Cote et al. 2010a). Part of the difficulty in incorporating personality into dispersal historically was the skepticism that behavioral syndromes may play an integral role in ecological processes (Crews 2013). Here, I have shown that *Notonecta irrorata* exhibits a behavioral syndrome in foraging behaviors that is also related to an individual's propensity to disperse.

It appears that dispersal patterns based on personality might be different depending on the organism. There is support for the idea that bolder, more aggressive individuals, will disperse farther and more frequently than less aggressive individuals (Fraser et al. 2001; Cote et al. 2010a; Chapman et al. 2011). However, other studies have found that shy, passive individuals are more likely to disperse (Cote et al. 2010b; Found and St. Clair 2016). These studies cross a wide range of organisms. I found that within *N. irrorata*, passive individuals had a higher propensity to disperse earlier than did bold individuals.

In some cases, individuals that disperse further tend to be more asocial (Cote et al. 2010b). Asocial individuals can even have increased fitness at lower densities and would benefit by dispersing to a lower-density habitat (Cote et al. 2008). The passive *Notonecta* (which swim less

often, hide in vegetation more, and perch deeper in the water column than bold individuals) in my research exhibited many of the same behaviors that other studies found to be correlated with asociality. Previous studies found that 1) sociability in individuals was correlated with boldness, activity level, and shorter latency to emerge (Cote et al. 2010b), 2) refuge use in sociability tests was (negatively) correlated with boldness in risk-taking tests (Le Galliard et al. 2015), and 3) activity level, boldness, and sociality were all correlated with each other in young lizards (Le Galliard et al. 2015). My results then support the hypothesis that individuals with more asocial traits are more prone to disperse.

The hypothesis that more active animals have a higher resting metabolic rate (RMR) (Reinhold 1999) could explain why bolder *Notonecta* are slower to disperse. Dispersal is an energetically-costly behavior (Reinhold 1999; Bonte et al. 2012) and being more metabolically active could mean having less energy for dispersal. Therefore, if less active individuals have a lower RMR as hypothesized (Reinhold 1999) then passive individuals should have more energy available for dispersal. This reasoning supports my results that passive *Notonecta* disperse sooner than bold individuals.

Notonecta are known to increase their dispersal propensity in response to the perception of a greater predation risk (McCauley and Rowe 2010). The results of this study demonstrate that they also have the ability to assess the behavioral tendencies of conspecifics in order to determine whether or not to disperse. This is evident by the fact that all individuals, regardless of their personality type, were significantly less likely to disperse (on days 2 and 3 post-introduction) when there were more bold individuals present. One reason for this is that an abundance of bold individuals might be an indicator of patch quality. The presence of more active, bold individuals may imply to other individuals that patch resources are more abundant and can support many

individuals. It could mean that there are enough prey present to support highly-active individuals, or likewise, that there are few predators around. A high number of bold individuals in a patch also means that there are more encounters between individuals, and these increased encounters could be an explanation for a longer time to dispersal when there are more bold individuals present. Many animals exhibit this kind of "informed dispersal", where the individual gathers information to use before and during the dispersal decision (Clobert et al. 2009).

The *N. irrorata* dispersal rates for each BT were different only after two or three days of being in the patch. This time between the initial introduction to the pools and any observable difference in the dispersal rates of each BT might be due to individuals taking enough time to assess the habitat quality of the patch. Optimal foraging theory implies that it would not benefit an individual to prematurely leave a patch that was of sufficient quality (a behavioral false-positive result, of sorts), because dispersing again immediately upon entering a patch would be energetically-costly (Charnov 1976). However, if the individual can quickly assess the quality of the patch as poor then it will likely disperse to find a better patch. In the case of *Notonecta*, having more bold individuals present may have weakened the ability of any one individual to assess the pond quality, since all individuals were less likely to disperse when there were more bold conspecifics present in the pond.

If individuals of a species differentially disperse based on personality dynamics as my work and that of many others has shown then this non-random likelihood of dispersal could have large effects on colonization success, meta-population dynamics, and even community and meta-community dynamics (Clobert et al. 2004; Lapiedra 2016; Start and Gilbert 2017). Less social individuals tend to cope better with low initial population densities and have better colonization success (Canestrelli et al. 2016). Having more active predator individuals in a patch can also

dramatically change the prey composition (Royauté and Pruitt 2016; Start and Gilbert 2017). Similarly, prey personalities and predator species can interact in a way that affects prey mortality, and these personality compositions combined with predator hunting mode can be important predictors of predator-prey interaction strength (Belgrad and Griffen 2016). All of these examples are ways that the personality dynamics of individuals can have an effect on the population of individuals as well as the community dynamics of the pond.

My results suggest the need for a more nuanced approach to evaluating dispersal, meta-population dynamics, and colonization success in animals. Simple dispersal models where each individual of a species is treated as the same are useful and necessary in some situations, such as using as a baseline to develop more complex models or to simplify concepts for education and cross-disciplinary use. However, in order to strengthen our applications of dispersal dynamics we need 1) a more predictive framework, in which one could evaluate the likelihood of dispersal or colonization success based on personality dynamics, and 2) more practical tools that managers and conservationists could use to better sustain animal populations. Invasion biology, spatial ecology, and conservation are all disciplines that would benefit from applying behavioral data (e.g. Lapiedra et al. 2016; Travis and Dytham 2002; Spiegel et al. 2017; Found and St. Clair 2016). Since my work and that of many others has shown that behavioral syndromes can shed light on dispersal patterns, animal management practices (reintroduction programs, establishment of corridors, aiding migration, sustaining meta-populations, etc.) (Merrick and Koprowski 2017) and environmental planning would greatly benefit from studying and incorporating animal personalities and their influence on dispersal.

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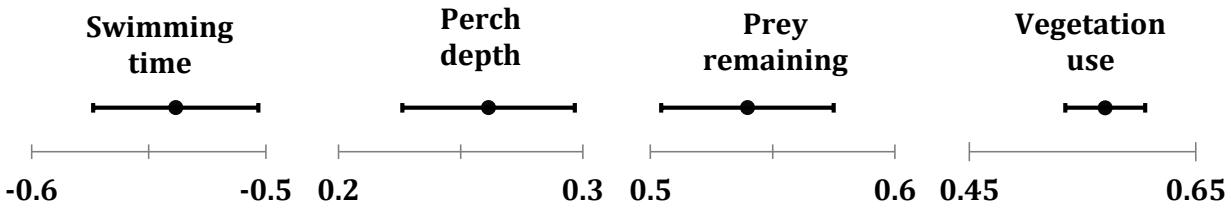

Figure 1.1: Average PC1 loadings (± SE) across two blocks for each behavioral trait included in the Principal Components Analysis. 'Swimming time' was negatively correlated with PC scores, while 'prey remaining' and 'vegetation use' were the most positively correlated with PC score.

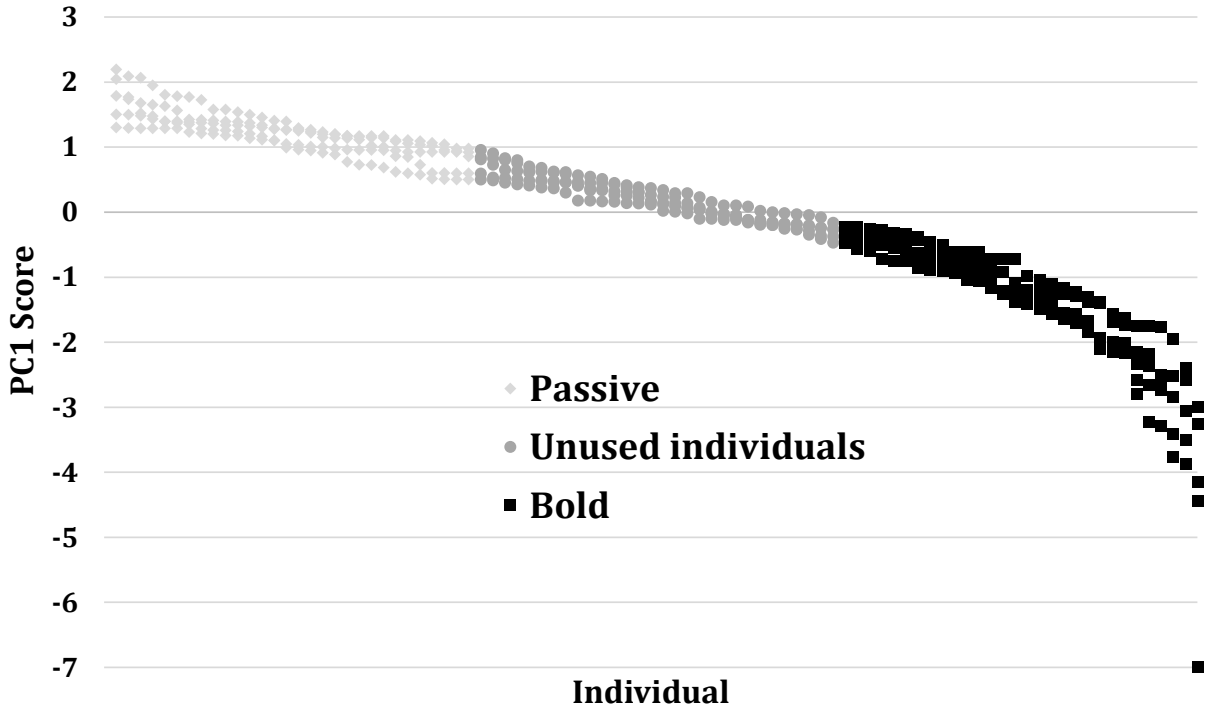

Figure 1.2: Distribution of PC scores for all individuals in this study. The order of individuals along the x-axis is based on the rank order of their PC1 score. The top third of scores in each PCA were assigned the personality type of "passive", while the bottom third of scores in each PCA were assigned the personality type of "bold". The individuals with scores in the middle were not used.

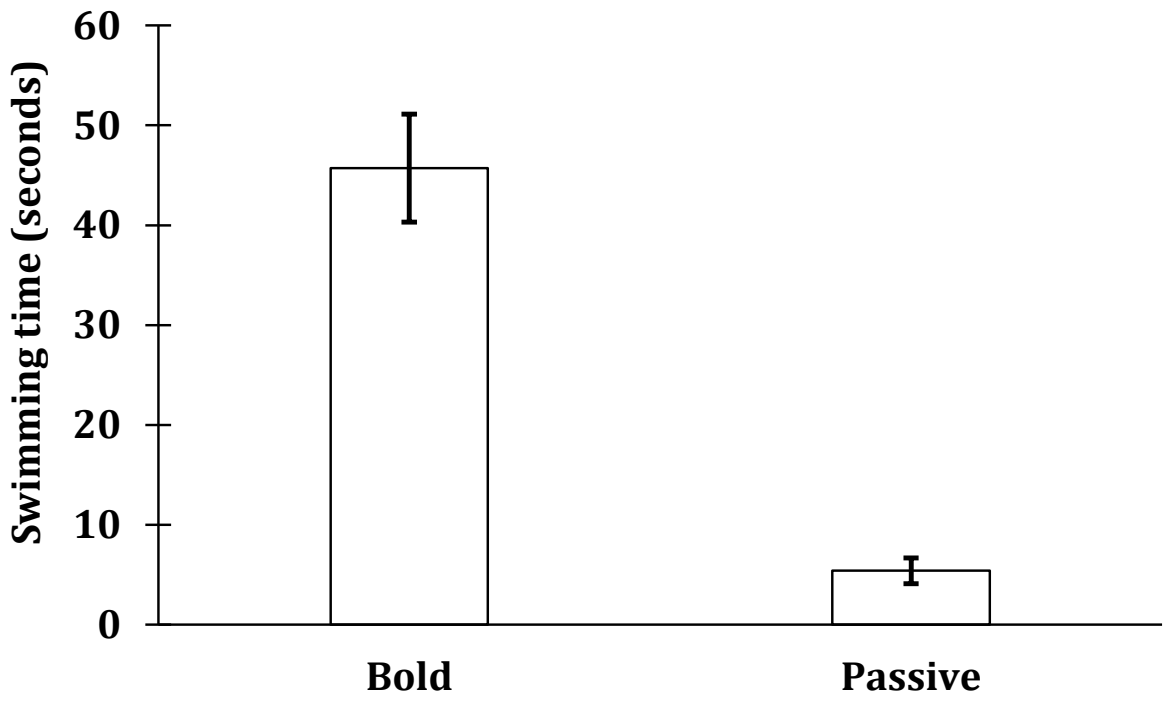

Figure 1.3: Average swimming time (± SE) of bold and passive individuals during their 10 minute observation period.

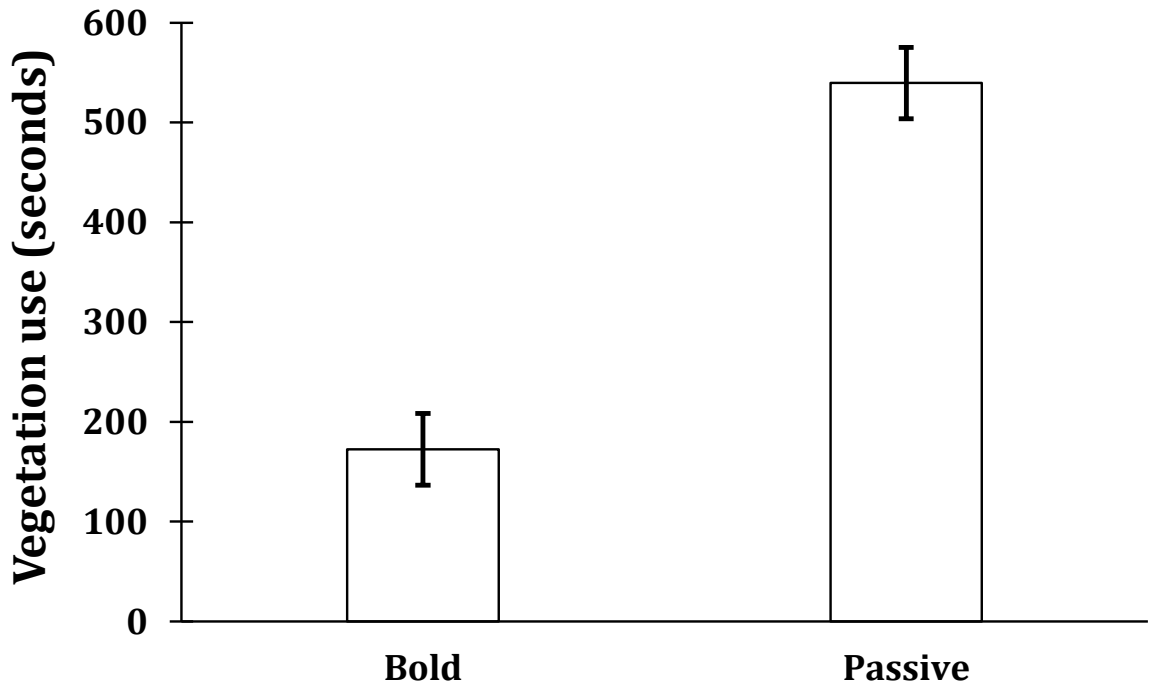

Figure 1.4: Average amount of vegetation use (± SE) by bold and passive individuals. Vegetation use was defined as any individual swimming amongst, resting in, or perching in the artificial vegetation.

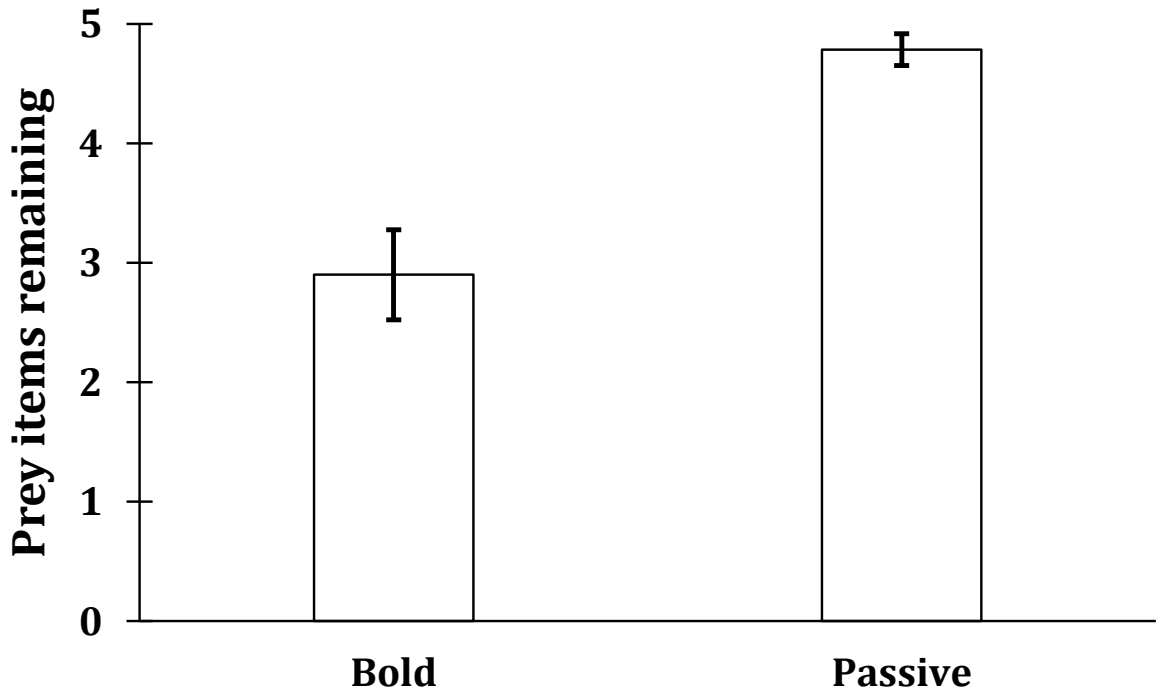

Figure 1.5: Average (± SE) number of prey items left uneaten (out of a maximum of five) by bold and passive individuals.

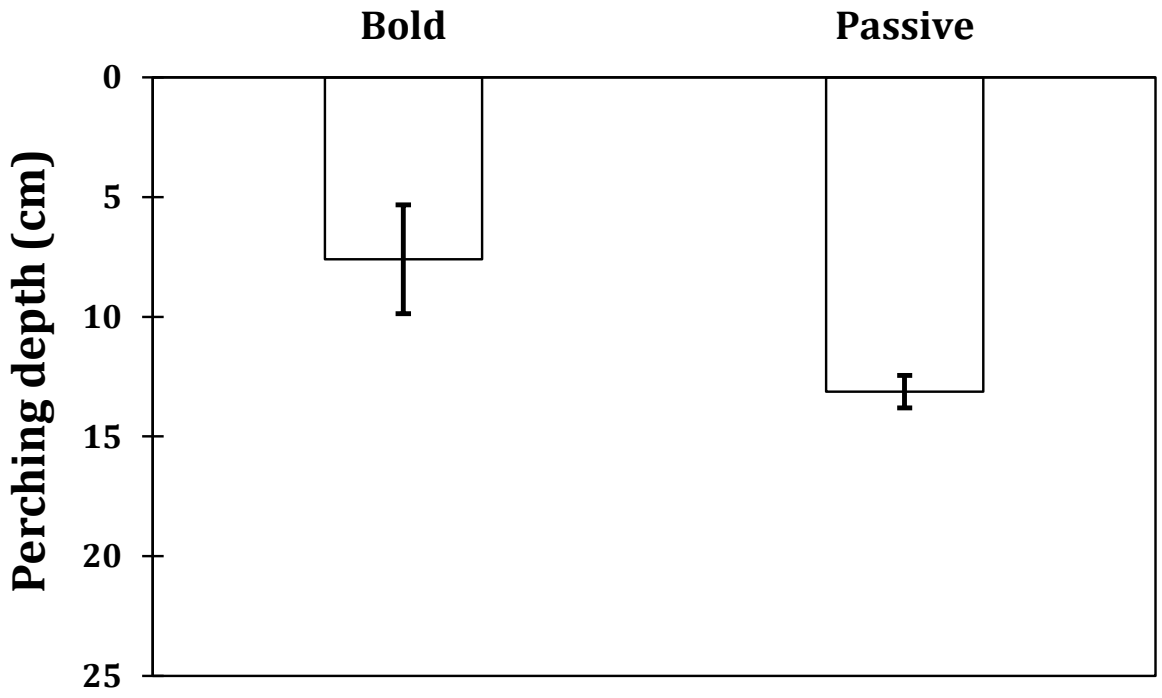

Figure 1.6: Average perching depth (± SE) of bold and passive individuals. Perching depths were weighted by how long an individual remained at that perch. Total depth of the aquaria was 25 centimeters.

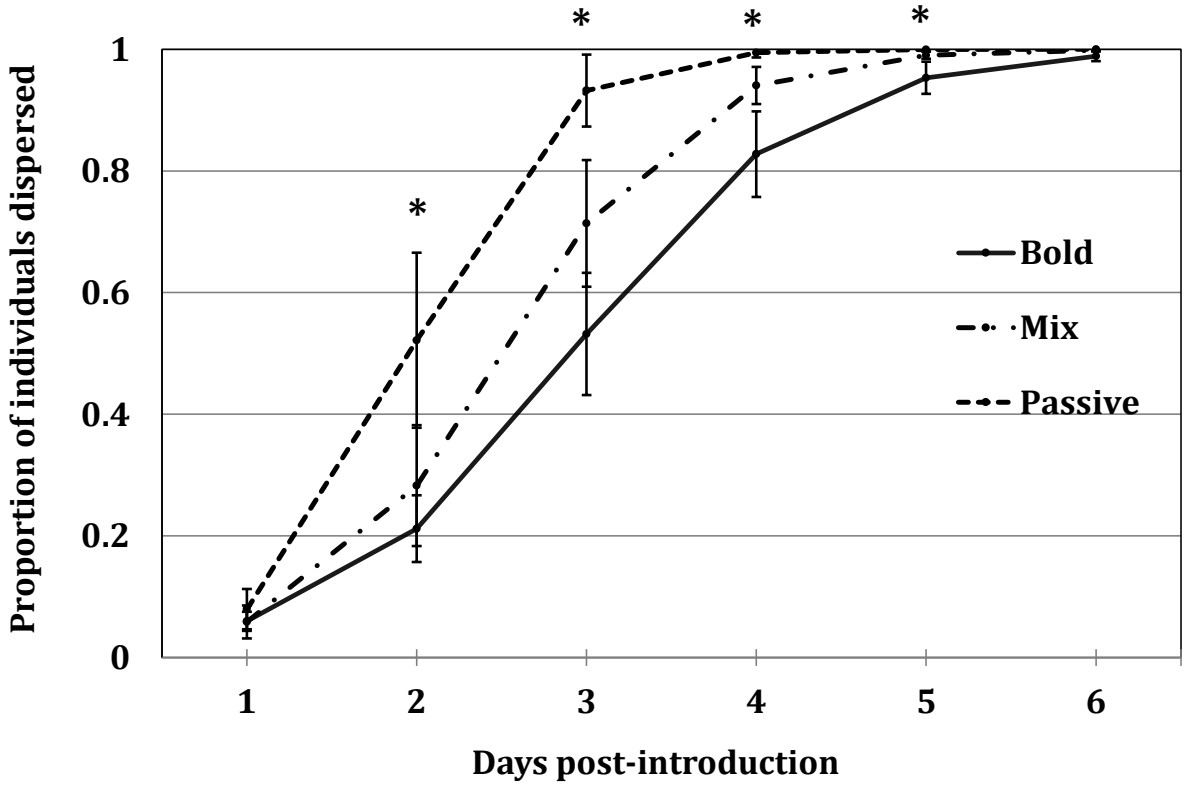

Figure 1.7: Cumulative proportion of individuals (± SE) that dispersed from treatment pools on each of six days after individuals were initially placed into pools. Days marked with asterisks signify days in which the proportion of individuals that dispersed was significantly ($p \leq 0.05$) higher in the passive treatment than in the bold treatment. The proportion of individuals that dispersed in the mixed treatment did not differ significantly from that observed in either the bold or passive treatment on any given day ($p \geq 0.0918$).

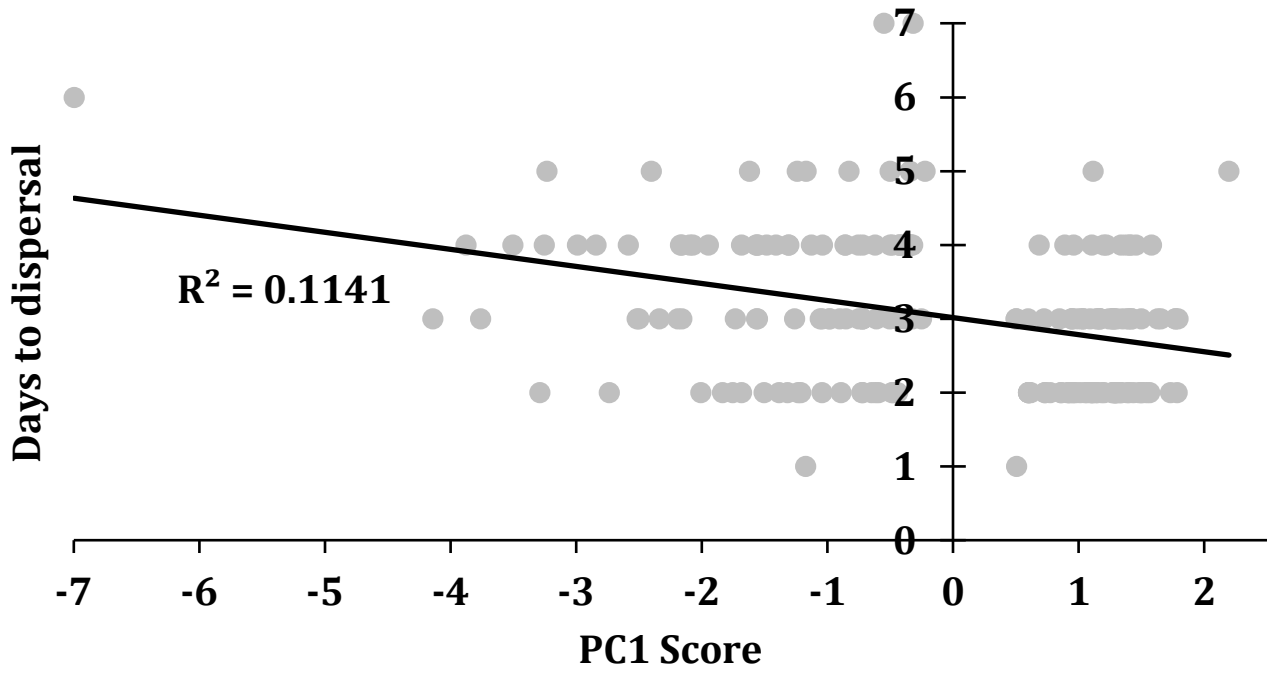

Figure 1.8: Day of dispersal based off each individual's PC score in the bold and passive treatments. Each circle represents an individual that was selected for the dispersal experiment. Individuals classified as passive had PC1 scores > 0, while those categorized as bold had PC1 scores < 0.

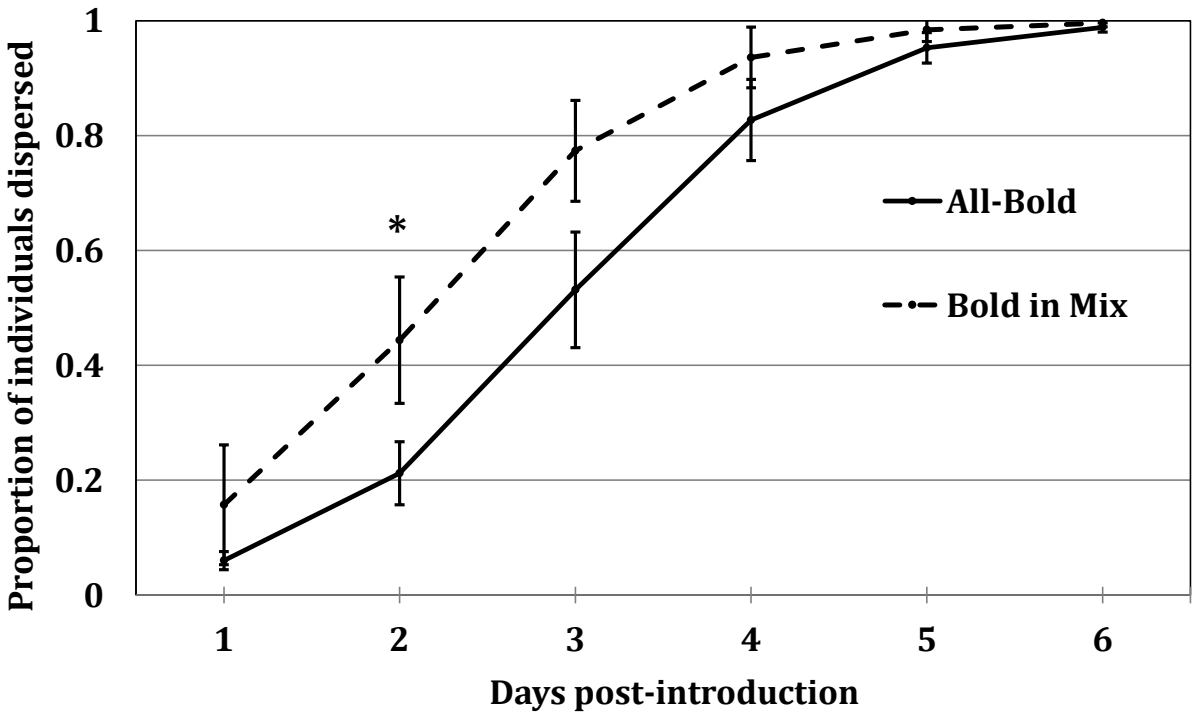

Figure 1.9: Proportion of bold individuals dispersed from all-bold vs mixed treatments (± SE). All-bold and mixed treatments differed on day 2. Days marked with asterisks signify days in which the proportion of bold individuals that dispersed was significantly ($p \leq 0.05$) higher in the mixed treatment than in the all-bold treatment.

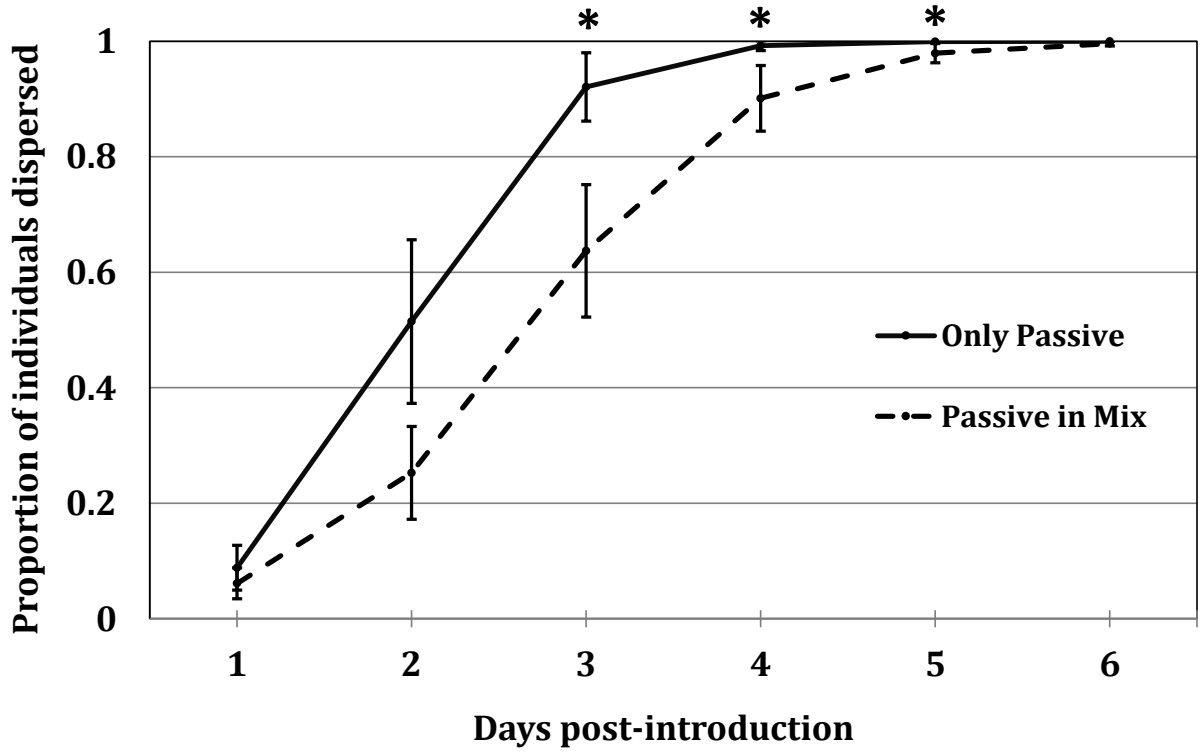

Figure 1.10: Proportion of passive individuals dispersed from all-passive vs mixed treatments. All-passive and mixed treatments differed beginning on day 3. Days marked with asterisks signify days in which the proportion of passive individuals that dispersed was significantly ($p \leq 0.05$) higher in the all-passive treatment than in the mixed treatment.

CHAPTER II

INTRODUCTION

It is well-documented that behavior (e.g., foraging, mating, or resource use) can vary substantially among individuals within a species (Duckworth 2006; Kralj-Fiser and Schuett 2014) and can depend on environmental context (Wilson and Krause 2010; Royauté et al. 2014). However, when an individual is predisposed to multiple behaviors that are correlated with each other the suite of correlated behaviors can be referred to as personality, or a "behavioral syndrome" (Sih et al. 2012). Behavioral syndromes can be represented as an axis of change across a suite of correlated behaviors and the position of individuals along this axis defines the individual's behavioral type (i.e., the specific combination of behaviors displayed by a particular individual; hereafter BT) (Sih et al. 2004). For example, opposite ends of this axis could correspond to individuals that are less likely (i.e., passive) or more likely (i.e., bold) to engage in a broad suite of correlated behaviors (Sih et al. 2003). Though the terms "behavioral syndrome" and "animal personality" are generally used to describe the same thing, I use the term "personality" throughout when describing behavioral syndromes in order to avoid confusion.

The idea of personality in animals is debated (Beekman and Jordan 2017). Part of the skepticism is that some behavioral studies only measure one behavior, not correlations among many, and other studies do not measure the repeatability of these behaviors through time and contexts. In order to test for the presence of personality, one needs to evaluate 1) correlations among many behaviors, 2) the consistency in levels of behaviors through time, and 3) the consistency in levels of behaviors across different contexts.

If individuals have a personality, they should exhibit consistent correlated behaviors through time (repeatability). Even though the levels of any one behavior will fluctuate over time we should expect to see the same relative levels if an individual's behaviors are measured at different times. For example, an individual defined as "bold" based on its behavior at one point in time should exhibit the same "bold" behavioral tendencies at another point in time. If the measured behaviors change in such a way that "bold" individuals at one point in time act as "passive" individuals at another point in time then these personality definitions would be obfuscated.

Behaviors also need to be consistent either within or across different contexts in order for them to be defined as personality. Animals experience many different types of contexts ranging from environmental variation, different demographic makeups, or different predation levels. These contexts can affect how an individual behaves. For example, in reef fish individuals of one particular species might be more active overall when the temperature in their environment is low and less active when the temperature is high (Nowicki et al. 2012). Similarly, individuals of a certain species might be less active overall when the threat of predation is high compared to when it is low (Lawler 1989). These examples can still describe personality within the species, despite individuals changing their behavior, if the difference in behaviors among personality groups remains consistent within a given context; that is, if the relative levels of behavior between individuals of different personality types remains the same.

Alternatively, the type of individual and the context it is in might have no effect on that individual's behavior. For example, bold individuals might act just as bold regardless of the threat of predation level, and passive individuals might remain passive even if the predation threat is low. If individuals exhibit the same behavioral scores no matter what context they are exposed to then this would support the notion that personality characteristics are consistent.

The presence and personality type of conspecifics could be a form of contextual variation that has an effect on an individual's behavior. Individuals might alter aspects of their behavior depending on who is around them. For example, if two bold individuals encounter one another, one may change its foraging behaviors to act slightly more passively in order to avoid resource competition, aggressive interactions, or shared habitat use. Similarly, two passive, inactive individuals together might encourage one individual to act bolder as a way of exploiting the resources or habitat use that are available due to the other individual's passive nature. The same idea could be apparent in a situation in which a passive individual acts *more* passive when in the presence of a bold individual, or vice versa. These examples would still be evidence for a behavioral syndrome if the two personality groups maintained a relative difference in their levels of behavior within each context. Alternatively, individuals might not alter their level of behavior in the presence of other individuals due to the personality constraint on behavior. Instead, an individual might maintain its personality across contexts regardless of the situation. We would then expect individuals to maintain a consistent level of behavior no matter which conspecifics are around them.

Relatively few studies have looked into the potential presence of personality in invertebrates, despite invertebrates making up the vast majority of animals on the planet (Kralj-Fiser and Schuett 2014). Thus, to examine questions regarding 1) whether correlated traits comprise a behavioral syndrome and 2) whether these personalities are consistent through time and across situations, I used a species from the genus of semi-aquatic backswimmer insects, *Notonecta*. *Notonecta* are predatory insects that live in ephemeral and permanent pond communities. Both adults and larvae spend the majority of their time in the water, but adults are capable of flight and can disperse long distances (McCauley and Rowe 2010). Individuals can

complete their lifespan within a single habitat patch but can also make the decision to leave a patch and search for a new one if so inclined (McCauley and Rowe 2010). *Notonecta irrorata* is the largest species of *Notonecta*, typically averaging 13.7 mm in length (Streams 1987), and is commonly found throughout the Eastern United States. They generally swim and forage at the surface of ponds and rest further underwater near pond bottoms (Streams 1987). Their size and general behavior makes *N. irrorata* an ideal organism to use in order to study aspects of personality. If personalities do exist in *N. irrorata*, I would expect to see correlations among various foraging traits. Previously, I examined personality in *N. irrorata* to determine if there were correlations between different foraging behaviors (swimming activity, vegetation use, perching depth, and prey consumption) and whether personality was also associated with dispersal propensity (Chapter I). In order to assess whether these personality traits were consistent through time and across all individuals, I documented the same behaviors another time with a different collection of individuals. If personalities are consistent through time and across contexts, I expect that individuals would 1) exhibit similar correlations between behaviors as documented before, 2) maintain their levels of behavior through time, and 3) maintain their levels of behaviors even in the presence of different conspecifics.

MATERIALS AND METHODS

I performed a set of experiments to evaluate the hypotheses that 1) different foraging behaviors would be correlated across individuals as such a correlation would provide evidence of a behavioral syndrome, 2) the levels of different foraging behaviors would be consistent through

time within a particular context, and 3) the foraging behavior of an individual will not change when other individuals of the same or different behavioral type are present.

Test for Behavioral Syndrome

To test the hypothesis that *N. irrorata* exhibited a behavioral syndrome, I conducted behavioral assays on individuals by observing four common foraging behaviors: 1) time spent swimming, 2) time spent using vegetation for swimming, resting, or perching, 3) prey foraging efficiency, and 4) average perching depth in the water column (weighted by time spent at each perch). Choosing when and for how long to swim as well as whether or not to utilize vegetation in the water are two of the most common behaviors *Notonecta* have to perform, and the efficiency at which an individual *Notonecta* consumes prey items is also an important behavior for survival. The regularity and importance (Bennett and Streams 1986; Streams 1987) of these three traits makes them ideal behaviors to observe and measure. Correlations between these behaviors may occur if individuals possess some quality that makes individuals more or less likely to exhibit levels of behavior that could be considered as bold. If an individual is more bold, then it will likely swim more, use vegetation less frequently, and seek to capture prey more frequently in a given time period. Swimming out in the open and seeking out prey is a risky suite of behaviors because it leaves an individual vulnerable to predation. Additionally, since the surface of the water is a riskier place to forage, those individuals that perch higher in the water column to forage for prey would be considered to be more bold.

I observed the foraging behavior of 60 *N. irrorata*. For logistical reasons, I performed two separate assays of 30 individuals each on two different days (each day is referred to as a block).

Collection for the observations took place in August, 2017. For each block, 30 *N. irrorata* individuals were collected over the course of one day from ponds in the Croatan National Forest (35°02'53.1"N 77°03'05.8"W). Individuals were placed in a common bucket when initially collected in the field but were each placed into their own labeled plastic containers filled with approximately 470 mL of pond water and one or two sticks to perch on immediately upon return to the lab a few hours later.

Behavioral observations on each individual were made either one or two days after collection. *Notonecta* were starved between time of collection and start of the behavioral observations. Each individual's behavior was observed in one of five 15-gallon aquaria (60 cm x 30 cm x 33 cm) filled 25 cm high with reverse osmosis treated (RO-rite) tap water. A simulated vegetative refuge was placed on one side of each tank by hanging 14 pieces of frayed coconut husk rope that extended from the top of the tank to the bottom. The vegetative refuge made up about 20% of the space in the aquarium with the rest of the space consisting of open water. All tanks were placed onto shelves and surrounded with black boards on three sides to prevent individuals from seeing one another. One side of each tank was left open so that I could observe each individual. Every tank had centimeter depth lines written in marker on each open side to facilitate the measurement of perching depth of individuals.

Each *N. irrorata* was observed in a tank for two separate five minute periods, once in the morning beginning at approximately 8 A.M. and once in the afternoon beginning at approximately 2 P.M., for a total observation time of ten minutes for each individual. After being placed into aquaria, individuals were allowed 35-40 minutes to acclimate before being observed (Streams 1987). Three behaviors (swimming time, vegetation use, and perching depth) were observed and recorded using the program JWatcher v1.0 (Blumstein and Daniel 2007). Swimming time was

measured as the amount of time an individual spent actively moving around the tank. Vegetation use was measured as the amount of time an individual spent associating itself with the artificial vegetation by either perching or swimming in it. Perching depth was measured as the average depth in centimeters an individual perched either on the vegetation or on the sides of the tank, weighted by the amount of time they spent at each perch. After the five minute period, the individual was dip-netted out of the water and put back into the plastic pint container, and a new individual was placed into the tank.

After observing the swimming, resting and perching behavior of *Notonecta*, I transferred each individual into their own 20 cm x 32.5 cm x 11.5 cm plastic container containing 470 mL of water and five 3rd to 4th instar larval *Aedes aegypti*. To estimate the foraging efficiency of an individual *Notonecta*, I counted the number of *A. aegypti* larvae eaten by *Notonecta* within four hours.

Once all behavioral data was collected for individuals within a block, I performed a Principal Components Analysis (PCA) on the correlation matrix for the four traits mentioned above. I used a PCA in order to reduce the four correlated traits into a smaller set of axes that could be interpreted. The first principal component axis (PC1), which always explains the greatest amount of variance in the data, represents a gradient of correlated behaviors and differences in PC scores among individuals reflect how they differ in these correlated behaviors. I refer to this axis as a "boldness" gradient because the correlations of behaviors with the scores of this gradient indicate that lower scores correspond to individuals that had more bold characteristics (higher swimming time, lower vegetation use, shallower perch depth, and less prey remaining; see results for details). In order to evaluate the differences in foraging behavior between different personality types, I separated individuals into two distinct personality groups. Individuals were sorted on the

basis of their PC1 scores and those with the highest 10 PC1 scores were classified as "passive" and those with the smallest 10 PC1 scores were classified "bold".

All analyses were performed in SAS Enterprise Guide (SAS Institute, Cary NC). In order to confirm that the two personality groups differed in their foraging behaviors, a comparison between the PC1 scores (response variable) among the two personality types was run using a generalized linear mixed model (GLMM). This method was used in order to treat block as a random effect and incorporate a block by personality interaction term. The model was fitted using restricted maximum likelihood estimation (REML) with a variance components covariance structure and the Kenward-Rogers method for computing denominator degrees of freedom. Comparisons of each behavior between the two personality types were run using the mixed procedure, treating personality as a fixed effect and block as a random effect.

Test of Consistency in Time and Context

I then tested the hypothesis that an individual's foraging behavior would change when another individual was present and would depend on whether the other individual present was considered to be bold or passive. To set up these experiments, five individuals of each behavioral type were randomly chosen to be "focal" individuals (the individual whose behavior I was measuring). These individuals were then observed in three additional separate assay treatments: 1) alone in the aquarium, 2) together with a bold individual, and 3) together with a passive individual. The order in which these assays were performed was randomly assigned for each individual. Aquaria were set up in the same way as in the first behavioral assays, and swimming time, vegetation use, and perch depth were recorded for the focal individual only. Prey foraging

efficiency was not measured in this set of experiments due to the logistics of measuring prey consumption with multiple individuals present.

To assess whether an individual's foraging behaviors remained consistent through time, I ran a set of paired t-test using PROC TTEST. Each pair consisted of the observed level of one behavior at two different points in time- once from the initial round of observations before they were assigned a personality type, and once when they were observed alone for a second time. A different T-test was performed for each foraging behavior.

To compare differences in the levels of behavior when an individual was alone to when an individual was with either a bold or passive individual, I ran a set of paired t-tests using PROC TTEST. Each pair consisted of the level of a behavior when the individuals were alone and the level of that same behavior when the individuals were either 1) with a bold individual or 2) with a passive individual. A different T-test was performed for each personality type and treatment combination (bold alone vs bold with bold, bold alone vs bold with passive, passive alone vs passive with bold, passive alone vs passive with passive).

RESULTS

The first principal component axis explained 50.40% of the variation in foraging behavior on average (among the two blocks) and all four behaviors loaded heavily on this axis (Figure 2.1). Swimming time was negatively correlated to PC1 scores, while the other three behaviors (vegetation use, prey remaining, and perch depth) were positively correlated to PC1 scores. In general, higher PC1 scores were associated with lower swimming time, higher vegetation use, higher number of prey remaining, and deeper perching depth.

On average, individuals classified as "bold" and "passive" differed on the basis of their Principal Component 1 scores ($F_{1,38}$ = 140.40, p = < 0.001), suggesting a difference in personality between the two groups. Individuals that were classified as "bold" spent more time swimming ($F_{1,37}$ = 25.34, p < .001), used vegetation less ($F_{1,37}$ = 34.54, p < .001), perched higher in the water column ($F_{1,37}$ = 9.18, p = .0045), and were more efficient at capturing prey ($F_{1,37}$ = 178.82, p <.001) (Figures 2.2-2.5) than individuals that were classified as "passive".

Individuals maintained a consistent level of all four behaviors through time ($t_9 \leq |1.59|$, $p \geq$ 0.1279). I did not observe significant evidence to indicate that bold focal individuals altered their behavior when they co-occurred with either a passive or bold individual ($t_9 \leq |1.30|$, $p \geq 0.2245$; Figures 2.6-2.9), with one exception. Bold focal individuals perched on average ~4 centimeters higher when they were with another bold individual than when they were alone (t_9 = -1.93, p = 0.0862; Figure 2.9), which is 16% of the entire depth of the aquarium. I also found little evidence to suggest that the behavior of passive focal individuals changed when either a passive or bold individual was present ($t_9 \leq |1.36|$, $p \geq 0.2055$; Figures 2.6-2.9).

DISCUSSION

Relatively few studies have examined personality in insects (Kralj-Fiser and Schuett 2014), despite animal personalities being documented in a wide variety of organisms, including water striders, zebrafish, spiders, and elk (Sih and Watters 2005; Moretz et al. 2007; Royauté et al. 2014; Found and St. Clair 2016). My work suggests that behavioral syndromes also exist in *Notonecta irrorata* (and potentially other *Notonecta* species that exhibit similar behaviors). This result adds

to the growing body of literature indicating that the phenomenon of personalities in animals is widespread (Sih et al. 2012; Belgrad and Griffen 2016; Start and Gilbert 2017).

One of the main critiques on the validity of animal personalities is that individuals rarely maintain a certain level of behavior through time or across contexts (Beekman and Jordan 2017). In fact, consistency in a level of a suite of behaviors is one of the fundamental differences that sets apart personality research from other behavioral fields such as game theory or behavioral genetics, which imply that an individual's behavior changes through time and across contexts. Recent studies have even found that behavior in animals with complex life-histories, such as amphibians, is consistent and repeatable across life stages (Wilson and Krause 2012). In the case of *N. irrorata*, individuals that were initially categorized with certain BTs on the basis of correlated levels of behaviors maintained the same levels of each behavior through time. Additionally, the PC1 loadings from the Principal Components Analysis (Figure 2.1) were very similar to PC1 loadings reported for similar analyses in Chapter I (Figure 1.1). These PCAs incorporated the same foraging behaviors but were run on different individuals at different times during the summer (Chapter I: May-August 2017, Chapter II: September 2017). There was also consistency in the average level (across blocks) of each behavior for both personality types among the different sets of individuals at different times. The consistency in the loadings for each behavior and their associated PC1 scores (Average variance explained from experiment 1 PCA: 42%, average variance explained from experiment 2 PCA: 50%) shows a conservation of the behavioral syndrome across time and provides further evidence for the repeatability of a correlated behavioral response among two different sets of *N. irrorata* individuals at different times.

Notonecta individuals also showed consistent behaviors in different contexts. In other words, bold individuals who were initially observed to swim more, use vegetation less, and perch

shallower maintained a similar level of swimming time, vegetation use, and perching depth when they were observed with other individuals present (Figures 2.6-2.9). Passive individuals also maintained the level of traits when together with other individuals that corresponded to their "passive" description (i.e. less swimming time, greater vegetation use, etc.) (Figures 2.6-2.9). Individuals did not interact with one another in the aquaria by any means that I could observe. There were no observed instances of fighting or chasing, rather, each *Notonecta* kept to itself. This result has some important implications. First, it provides further evidence for the idea that personalities impart a constraint on organisms, whereby an individual maintains a certain level of behavior across a suite of behaviors. This is an important finding because oftentimes personality experiments fail to ask whether proposed personality traits are consistent in other contexts (Stamps and Biro 2016). The results of this thesis suggests that, regardless of an individual's personality, *Notonecta* foraging habits are not influenced by other individuals.

Interestingly, I previously found that *Notonecta* dispersal rates were affected by the presence of more bold individuals in a pool; specifically, both bold and passive individuals increased their dispersal propensity when there were less bold individuals present (Chapter I, Figures 1.8 and 1.9). It appears that the presence of specific personality types of conspecifics has an effect on one behavior (dispersal) but not others (foraging). This difference in effect could be due to the number of other individuals that a *Notonecta* was surrounded by i.e. the encounter rate. *Notonecta* foraging behaviors were observed only when one other individual was present in the aquarium, while dispersal rates were measured from pools beginning with twenty individuals. This difference in conspecific density is important because it implies that an individual *Notonecta'*s behaviors are unaffected by the behavior of conspecifics at low densities, but they are affected by the conspecific behavior at higher densities. Recent studies found that personality composition is

more important than group size in determining collective foraging behavior in a species of spider (Keiser and Pruitt 2014), but my results indicate that the population density could have an effect on an individual's behavior just as considerably as the composition of personality types.

Evaluating *Notonecta* foraging behaviors on a larger scale would be helpful in order to evaluate whether or not population density has an effect on any one individual's personality. Indeed, *Notonecta* live in high densities within ponds (Briers and Warren 2000) so future work with *Notonecta* should attempt to record foraging behaviors when many individuals are present in one area. While *Notonecta* did not alter their foraging behaviors when in the presence of one individual, they might alter their behavior when surrounded by many more individuals of a certain BT as they did with dispersal propensity in my study.

Comparisons of the behaviors of individuals between separate populations is another larger-scale study that could provide more insight into how the personality of individuals in the population affects population and community dynamics. Ponds where *Notonecta* are found generally make up a meta-population of individuals that disperse from nearby ponds and colonize others. These dispersal and colonization events likely change the personality composition of *Notonecta* within a pond at any given time, and thus the community dynamics of these ponds (Blaustein 1998). Indeed, many species of *Notonecta* have a strong effect on freshwater community structure (Murdoch et al. 1984; Blaustein 1998), and their presence and abundance can alter the zooplankton community (Shurin 2001), mosquito oviposition site selection (Eitam and Blaustein 1998), and densities of other invertebrate species (Blaustein 1998). Since *Notonecta* have different personalities with respect to foraging behaviors, populations with different personality compositions might differ in their effects on freshwater communities. For instance, a community with a population of mainly passive *Notonecta* might have a greater abundance of

zooplankton than a community with mainly bold *Notonecta* since passive individuals do not consume prey as quickly as bold individuals do. Alternatively, a pond with a population of mainly bold *Notonecta* might result in a smaller density of other invertebrates if the bold *Notonecta* are superior resource exploiters. A higher proportion of bold *Notonecta* within a pond could also encourage predators of *Notonecta* to colonize the pond more than one consisting of mainly passive *Notonecta* because bold individuals spend less time hiding in vegetation and more time higher in the water column where they are more conspicuous.

Knowledge of animal personalities should be incorporated into both models and practical applications. My results imply that integrating intraspecific behavioral differences into models is achievable, since individuals will maintain their personality differences across time and contexts. Additionally, there are clear differences in the foraging behaviors of *Notonecta* and presumably these differences would have differing effects on prey densities, resource space use, and other invertebrate behaviors. For example, since I found that different *Notonecta* BTs have different prey consumption rates, we might expect that individuals will have different attack rates and handling times. Future studies should test for differences in additional traits such as attack rate and handling time according to an individual's personality, including in other species and especially in traits that are frequently used in ecological models. Individual-based models (Grimm et al. 2006) would be an appropriate approach to incorporate intraspecific behavioral variation. Many classic models in ecology assume that individuals of one species can be lumped together (DeAngelis 2018), so utilizing individual-based models would allow differences within a species, such as personality, to be included. Many models have successfully used this technique to partition individuals on the basis of their size or age-class (DeAngelis 2018). Of course, future studies should investigate the consequences of using these more complicated models. For example, what

if there are interactions among parameters in which differences in personality affect attack rates or handling times in small individuals but the effect of personality is different in larger individuals? Answers to these types of questions still need to be explored.

In a practical sense, using behavioral knowledge has already shown some success in conservation initiatives (Buchholz 2007). Individuals with certain BTs have a better chance of survival post-reintroduction (Bremner-Harrison et al. 2004), while other individuals with certain BTs have a better chance of surviving in the face of anthropogenic habitat changes (McDougall et al. 2006; Powell and Gartner 2011).

This research lends support to the idea that individuals of a species should not be treated as identical copies. Many studies recognize the importance of intraspecific trait variation (Bolnick et al. 2011; Moran et al. 2016), but my research on *Notonecta* highlights the need for behavior (i.e. personalities) to be considered as another example of intraspecific trait variation (Wolf and Weissing 2012). This relatively new idea could strengthen our ability to make model predictions, discover new processes inherent in ecosystems, and aid in the conservation of animals.

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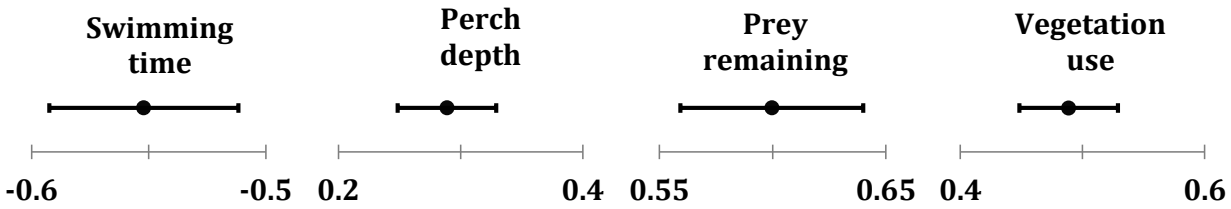

Figure 2.1: Average PC1 loadings (± SE) for each behavioral trait included in the Principal Components Analysis. 'Swimming time' was negatively correlated with PC scores, while 'prey remaining' and 'vegetation use' were the most positively correlated with PC score.

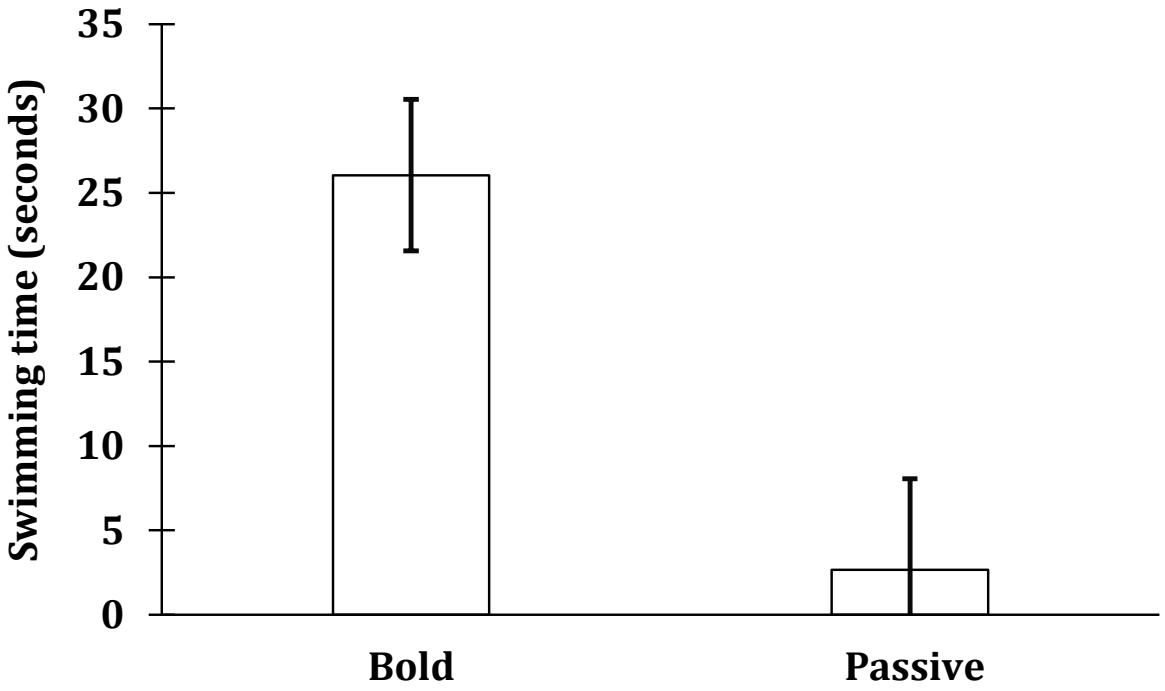

Figure 2.2: Average swimming time (± SE) of bold and passive individuals during their initial 10 minute observation period. An average bold individual swam almost 10 times as long as the average passive individual.

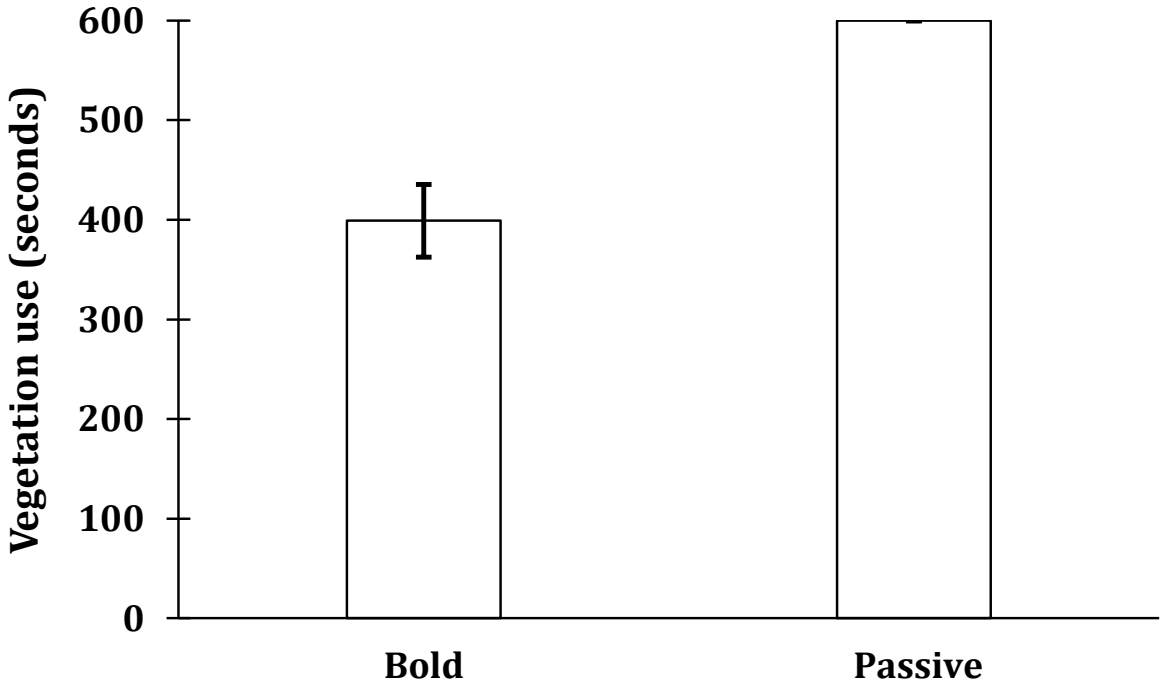

Figure 2.3: Average amount of vegetation use (± SE) by bold and passive individuals. Vegetation use was defined as any individual swimming amongst, resting in, or perching in the artificial vegetation.

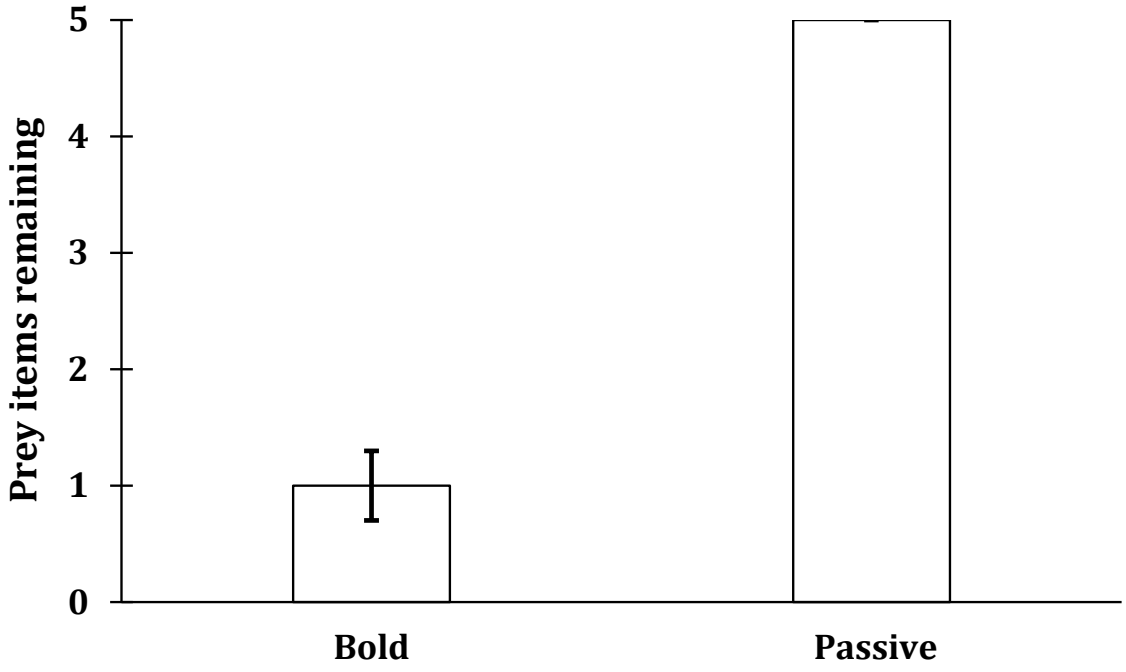

Figure 2.4: Average (± SE) number of prey items left uneaten (out of a maximum of five) by bold and passive individuals.

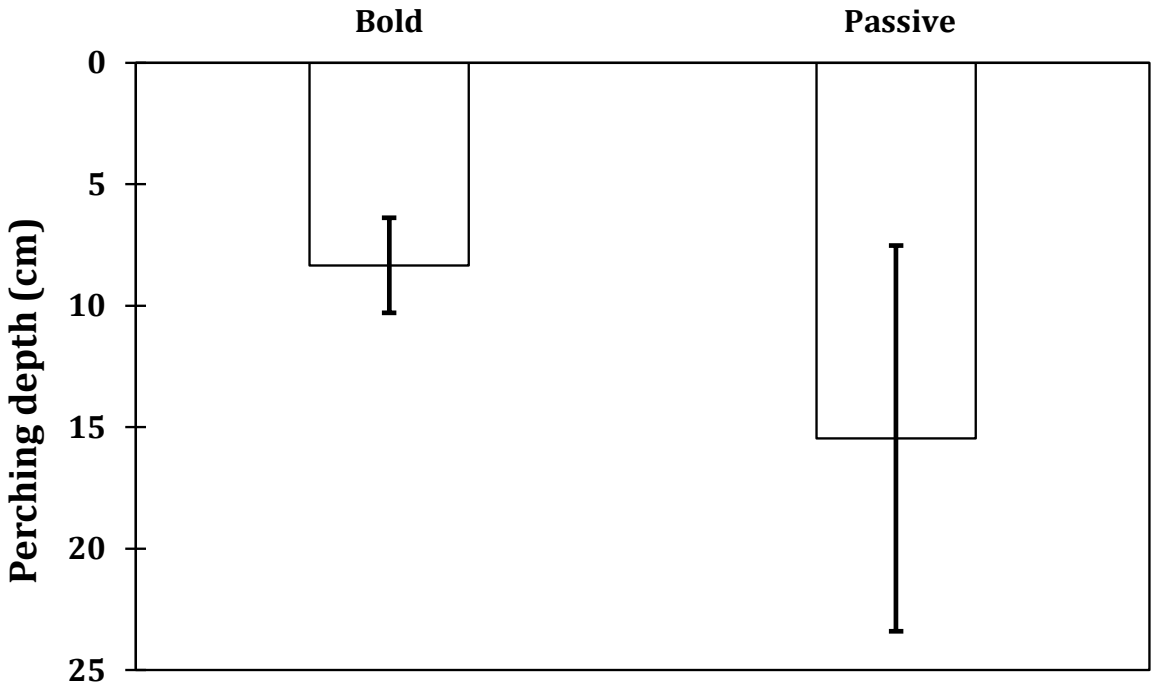

Figure 2.5: Average perching depth (± SE) of bold and passive individuals. Perching depths were weighted by how long an individual remained at that perch. Total depth of the aquaria was 25 centimeters.

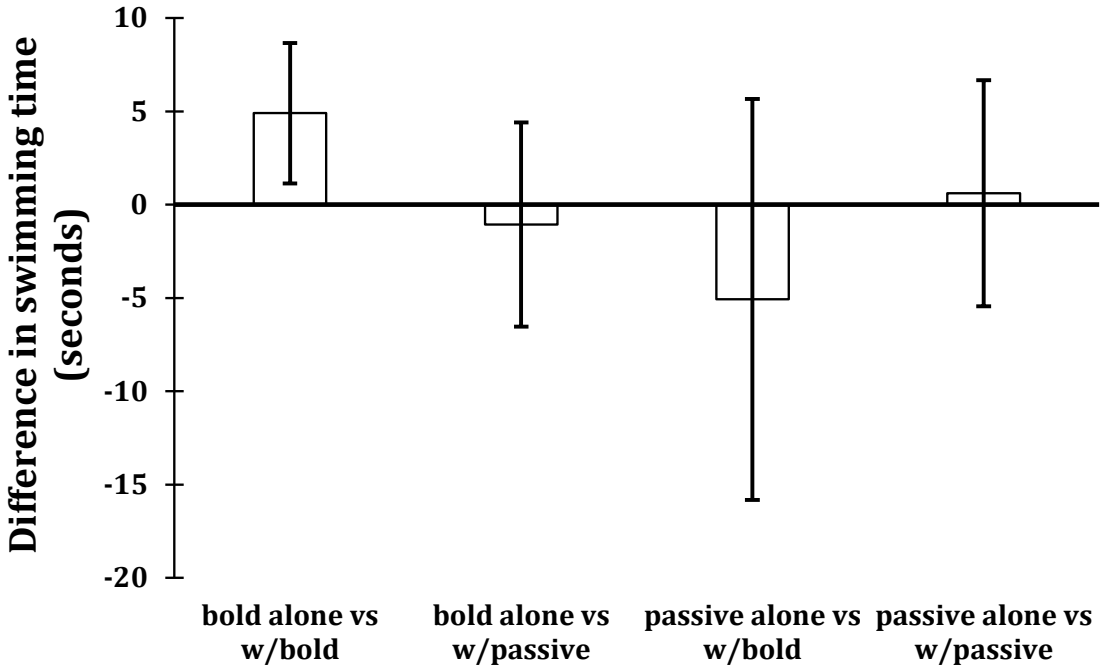

Figure 2.6: Difference in average swimming time (± SE) of bold and passive individuals when they were 1) with a bold individual and 2) with a passive individual compared to when they were alone. Swimming time did not significantly change among each situation.

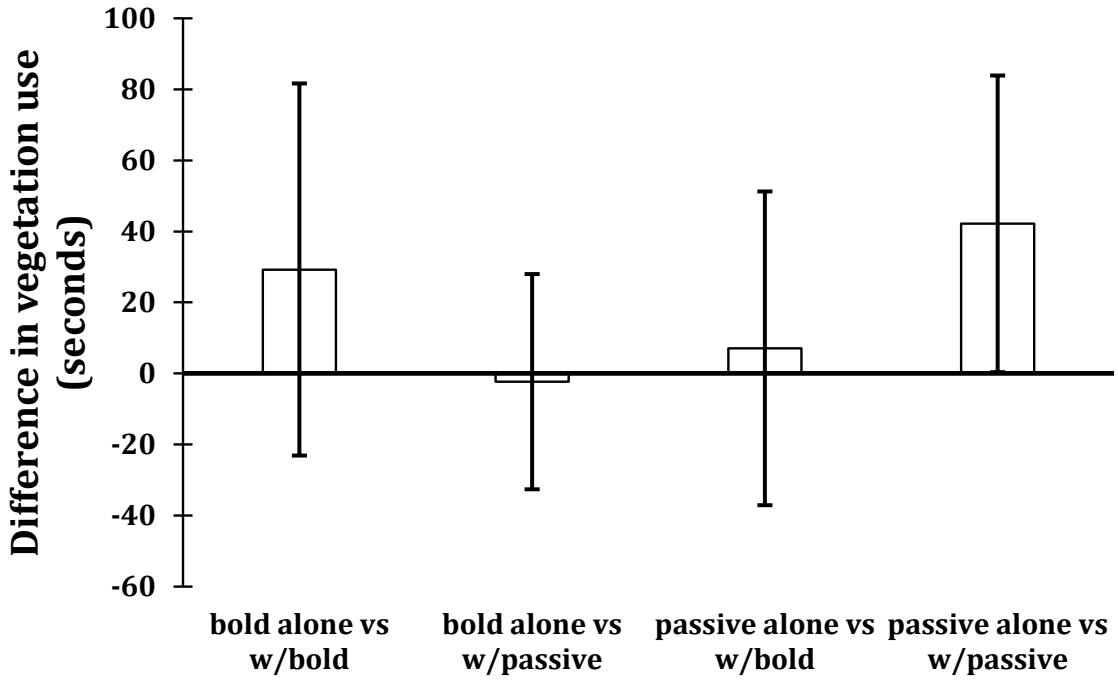

Figure 2.7: Difference in average vegetation use (± SE) of bold and passive individuals when they were 1) with a bold individual and 2) with a passive individual compared to when they were alone. Vegetation use did not significantly change among each situation.

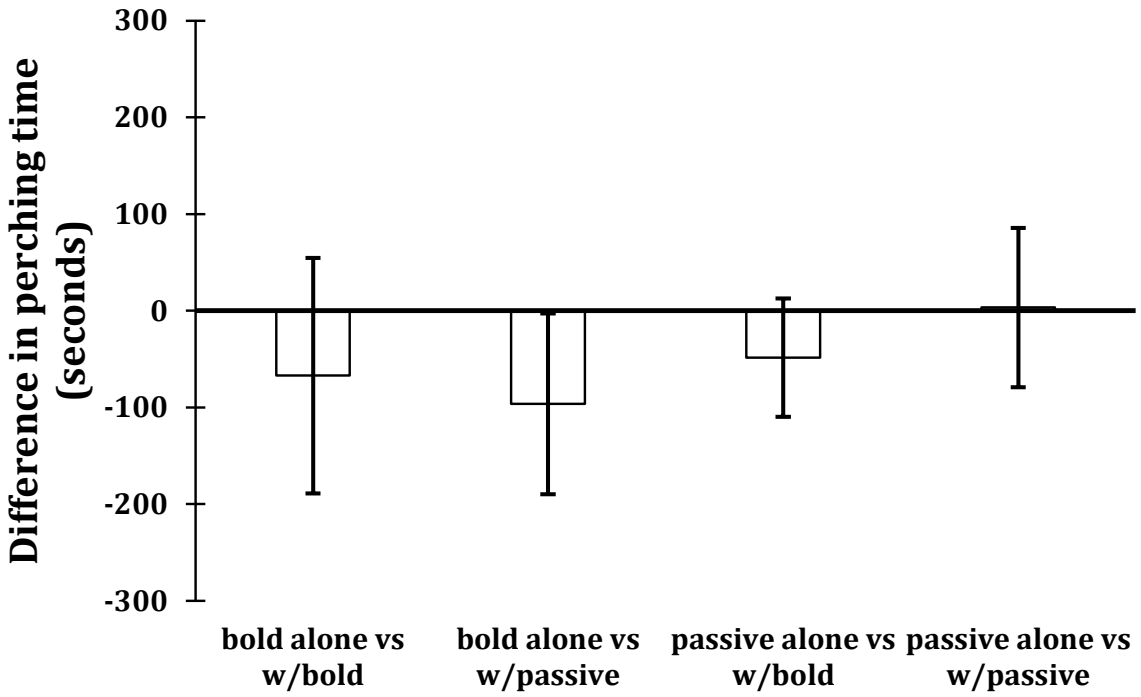

Figure 2.8: Difference in average total perch time (± SE) of bold and passive individuals when they were 1) with a bold individual and 2) with a passive individual compared to when they were alone. Perch time did not significantly change among each situation.

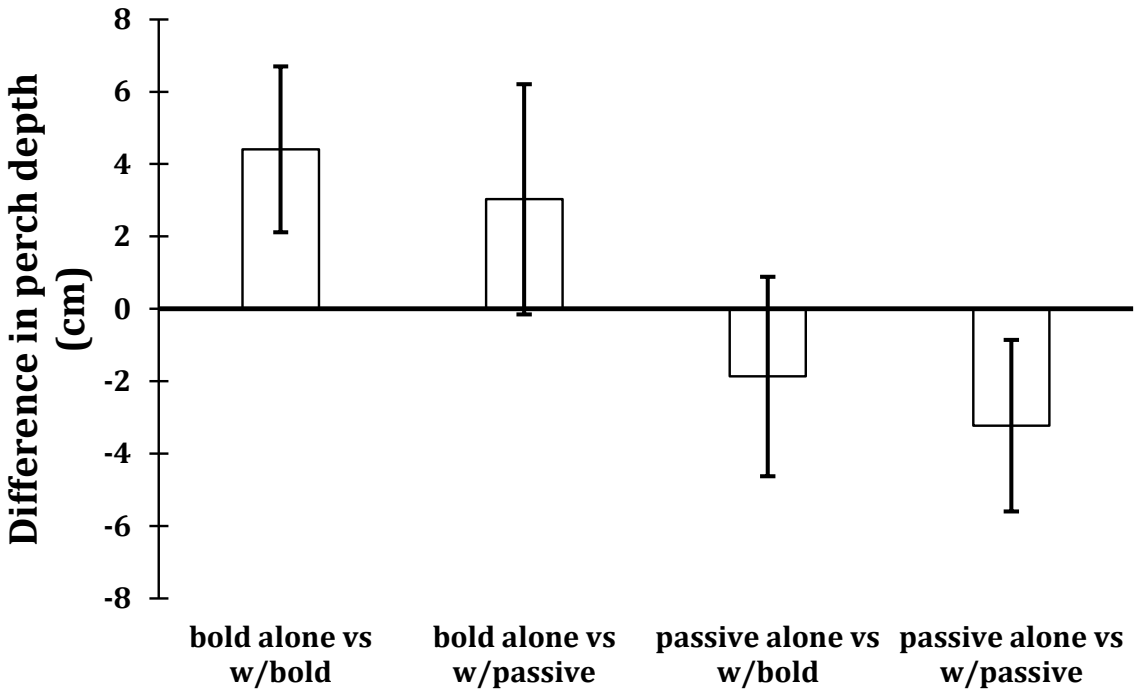

Figure 2.9: Difference in average perching depth (± SE) weighted by the time spent at each perch of bold and passive individuals when they were 1) with a bold individual and 2) with a passive individual compared to when they were alone. Perching depth did not significantly change among each situation.